

BIOLOGY OF *TANYCHELA PILOSA* (HYMEMOPTERA: ICHNEUMONIDAE), A PARASITOID OF THE AQUATIC MOTH *PETROPHILA CONFUSALIS* (LEPIDOPTERA: PYRALIDAE)¹

Wanda Jamieson², Vincent H. Resh³

ABSTRACT: *Tanychela pilosa*, a solitary endoparasite of the aquatic moth *Petrophila confusalis*, has hymenopteriform eggs that are oviposited in late summer or early fall, in the Clearwater River drainage of western Montana, USA. The first instar is a caudate-mandibulate type. Superparasitism may result from polyembryony but only a single wasp larva survives. Larvae undergo heteromorphosis as a third and final instar. Pupation occurs in the dry cocoon of the moth. Adult sex ratios approach 1:1. 72.2% of sites examined in the Clearwater River drainage had *P. confusalis* and 61.5% of these contained *T. pilosa*. Emergent rocks may enable ovipositing females to enter streams and search for caterpillars. Parasitization of *P. confusalis* reported from Idaho, Washington, and California may be by *T. pilosa*.

Hymenoptera parasitizing aquatic insects are rarely encountered in collections of stream insects. In an earlier study, we discovered that a population of the aquatic lepidopteran *Petrophila confusalis* (Walker) was parasitized by an aquatic wasp (Resh and Jamieson 1988) in Owl Creek, Missoula County, Montana (Fig. 1). The rate of parasitism in the moth population ranged from 55% at the outlet of Placid Lake into Owl Creek to 0% less than 5 km downstream from the lake outlet. Wasp pupae were identified as *Tanychela pilosa* Dasch, the type specimen of which is from Mexico (Dasch 1979).

In our original study, we indicated that parasitism occurred during the pupal stage of the aquatic moth, as has been reported for the agriotypid (now generally considered a subfamily of the Ichneumonidae) wasp *Agriotypus armatus* Curtis that parasitizes the caddisfly *Silo pallipes* (Fabricius) in Europe (Elliott 1982). In retrospect, if this supposition were correct we would have expected to see some type of activity indicating that moth pupae were being parasitized, such as adult wasps near the pupal patches that occurred on rocks in the streambed, or wasp eggs or larvae inside the moth pupae or moth cocoons.

Because of the lack of detailed information on hymenopteran parasites of aquatic insects (Hagen 1996), the present study was initiated to (1) describe the biology of the parasitoid *T. pilosa* and (2) document the distribution of *T. pilosa* beyond Owl Creek through surveys conducted in the Clearwater River drainage system of western Montana.

¹ Received October 11, 1997. Accepted January 12, 1998.

² Flathead Lake Biological Station, University of Montana, 311 Biostation Lane, Polson Montana 59860.

³ Division of Insect Biology, 201 Wellman Hall, University of California, Berkeley, California 94720-3112. Please send reprint requests to this author.

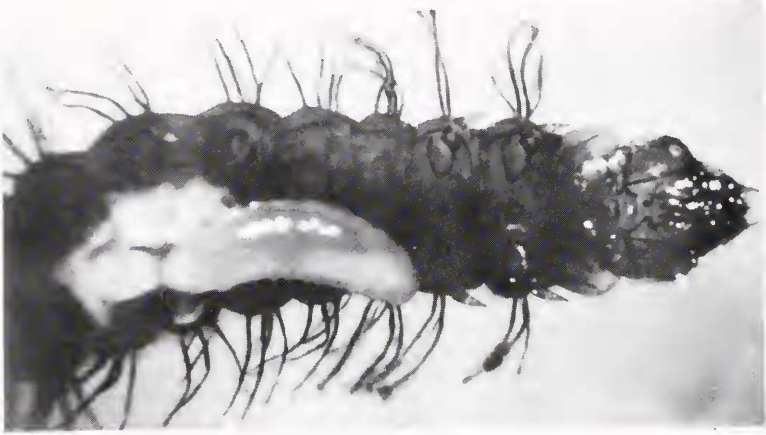


Fig. 1. *Petrophila confusalis* and its endoparasite *Tanychela pilosa*.

METHODS AND MATERIALS

In May 1989, lepidopteran larvae were collected from Owl Creek near the outlet of Placid Lake (Fig. 2). During the summers of 1993, 1994 and 1995, samples of approximately 100 *P. confusalis* larvae and pupae were collected randomly from various sites along the Clearwater River and its tributaries (Fig. 2).

Head widths of the moth larvae and prepupae were measured to determine instar classification; the caterpillars were then dissected to determine rates of parasitism. Wasp cocoons were dissected to determine stage of development and sex of the wasps. Life cycle observations were based on examinations of more than 1400 aquatic wasp larvae and pupae, the dissections of more than 1900 aquatic moth larvae and prepupae, and the examination of more than 2000 empty wasp and moth cocoons.

BIOLOGY OF *TANYCHELA PILOSA*

Egg stage: *T. pilosa* wasps are solitary endoparasites of *P. confusalis* caterpillars. The biology of the host (sometimes referred to as *Paragyraactis confusalis*) is described by Tuskes (1977, 1981), McAuliffe & Williams (1983), Bergey (1995), and summarized by Lange (1996). In late summer or early fall, the female wasp deposits an egg within the abdominal cavity of the moth larva. The pale yellow, jellybean-shaped eggs, about 0.5 mm long and 0.2 mm wide, are the hymenopteriform type (Hagen 1964, Fig. 14a).

Larval stage: Parasitism could occur during the moth's free-living first instar or during its other larval stages that are spent beneath silken retreats that

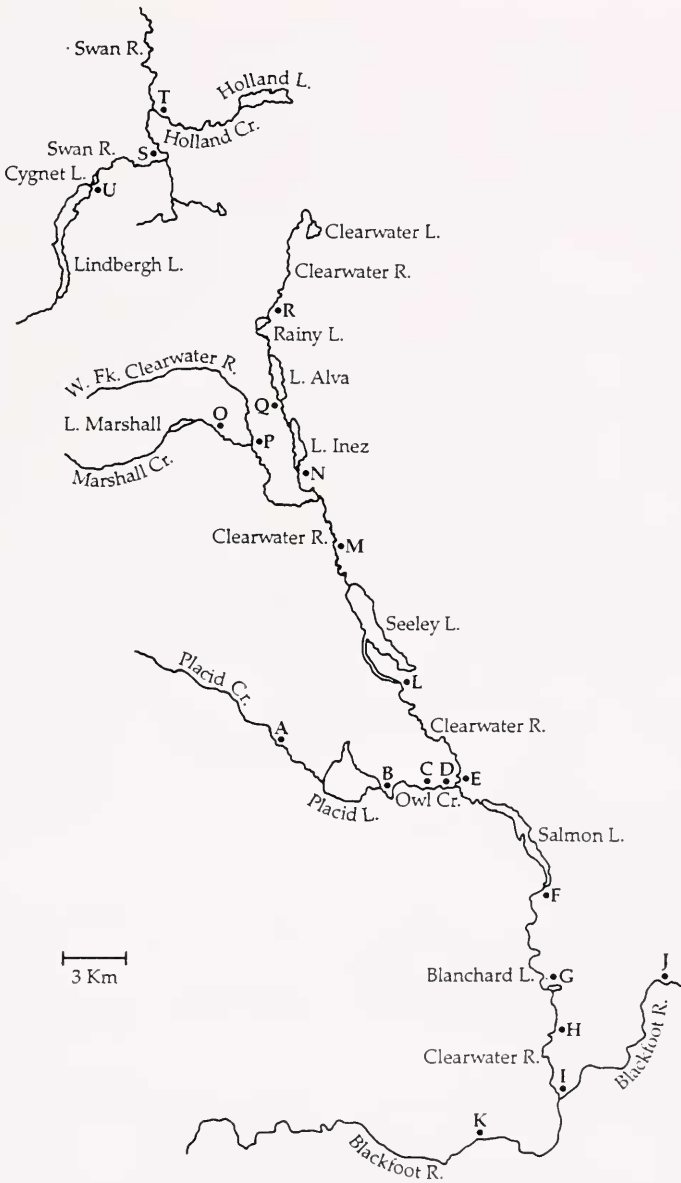


Fig. 2. Sampling locations in the Clearwater Drainage, western Montana, USA.

provide shelter (Lange 1996, Fig. 19.1). The free living, first-instar caterpillar is more vulnerable to predation and to dislocation (i.e., drift), and the duration of this stage is brief, e.g. first instars of *P. confusalis* occur in Owl Creek (Fig. 2) during a brief two-week period (McAuliffe & Williams 1983). In contrast, second, third, and fourth instars occur from mid-August to mid-October (McAuliffe & Williams 1983), and the female wasp could penetrate the silken covering of these instars with her ovipositor, laying her eggs within the host caterpillar.

The newly hatched wasp larva is less than 2 mm long. This primary or first instar is of the caudate-mandibulate larval type described by Hagen (1964, Fig. 18a, b, c). It has a brownish sclerotized head capsule with a black mandible. Its long, slender, segmented body is enclosed in a colorless, transparent integument; the internal body mass is bright yellow. A long "tail" that is almost equal in length to the rest of its body extends posteriorly from the dorsal portion of the wasp larva. Ulyett (1944) suggests the long tail may serve as one and/or all of the three following functions: an egg burster, a balancing organ to compensate for its large head, or for food absorption. Although the first instar wasp has mandibles, we found no evidence in any of the host larvae that internal tissues or organs had been damaged, nor did we ever observe any tissue attached to the mandibles of the wasp larva that would indicate it had been feeding. Apparently, the wasp larva absorbs food through its very thin cuticle from its host's hemolymph. Strands of fat bodies were noticeably reduced or absent in the hemocoels of parasitized caterpillars. Because there are no spiracles on the first instar larva, respiration is probably cutaneous.

T. pilosa overwinters in the first instar within its host. The wasp larva grows very slowly from October to June and growth appears to be relatively constant from year to year. For example, wasp larvae in samples collected from Owl Creek and the Lake Inez outlet (Fig. 2) on 23 Oct 1993 were very similar in size to the wasp larvae in samples collected during June 1994 and June 1995 from the same streams.

In areas where the rate of parasitism is high, two or more parasitoids may occur in one host (i.e., superparasitism). For example, of 44 moth larvae that were collected 23 Oct 1993 from Lake Inez (Fig. 2), 32 were parasitized. Of these, six (19%) caterpillars had been parasitized more than once; three of them had two larval parasites and each of the other three had three, four, and five parasitic larvae, respectively.

Several genera of Ichneumonidae that parasitize the eggs and larvae of Lepidoptera exhibit polyembryony (Hagen 1964, Chapman 1982) and this could account for the multiple *T. pilosa* parasitoids within the host *P. confusalis* caterpillar. We have not determined how long the different larvae within a single host live, but we have observed that eventually all but one die. For example, in a sample taken 15 Aug 1995 from the Lake Inez outlet (Fig. 2), one late-instar moth larva had 10 wasp larvae within its hemocoel. All wasp larvae were the same size, and had sclerotized heads and transparent body coverings, but only

one was wiggling; apparently nine of the wasp larvae had just died. Thus, this moth larva had been host to 10 wasp larvae for 9-10 months.

The dead wasp larvae can be found in the last abdominal segment; perhaps, the wiggling motion of the caterpillar forces these dead larvae to the posterior end of the moth's abdominal cavity where they remain (and subsequently can be counted). We noted that when host caterpillars contained only one wasp larva, that larva was usually alive. The bodies of the dead wasp larvae become white and opaque; their sclerotized head capsules enabled us to distinguish them from the fatty tissues of the caterpillar.

Hagen (1964) reported that the number of larval instars among hymenopterous parasites is variable. However, there appears to be a tendency for ectoparasitic larvae to have five instars and endoparasitic forms to have fewer than five (and often three).

During the fifth instar of the caterpillar, the wasp larva grows rapidly and undergoes heteromorphosis (sensu Chapman 1982; Hagen 1964 refers to this as hypermetamorphosis). The sclerotized head capsule splits along the dorsal line and the wasp larva emerges from its exuvium with a new body form. The new segmented body is covered with a loose transparent membrane. The body internally is bright yellow. During this metamorphosis, the wasp larva abruptly changes from a slender 2-mm long caudate-mandibulate type larva to a fat, globular, grub-like larva that eventually grows to fill the thorax and abdomen of the 10-mm long caterpillar within four weeks. This grub-like larva may represent the third instar.

We examined the head-capsule width of approximately 100 caterpillars from sites D in 1993, and N in 1993 and 1995 (Fig. 2). No size-class differences were observed in parasitized and unparasitized caterpillars.

Pupal stage: Prior to its pupation, the *P. confusalis* caterpillar modifies its silken retreat on a rock surface to form a thicker, oval patch. This patch is referred to as the external pupal case in Resh and Jamieson (1988, Fig. 1). The patch has semicircular openings at the edge [as described by Lloyd 1914, 1919 for *Petrophila fulicalis* (Schaus)] and the caterpillar scores a C-shaped slit at the upstream end of the patch. Beneath the patch, the caterpillar spins a waterproof cocoon that provides a dry environment for the pupal stage. When it has completely enclosed itself within a cocoon, the caterpillar becomes an immobile prepupa. When examined externally, there is no indication whether or not the caterpillar prepupa is host to a parasite.

If parasitization has been successful (i.e. sometimes the wasp larva dies before heteromorphosis occurs), the wasp larva emerges from its host during the caterpillar's prepupal stage. During emergence, the thoracic and abdominal skin of the caterpillar appears to disintegrate within the cocoon. The head sclerites and other tissues of the moth fall to the posterior end of the cocoon as the wasp larva emerges from its host within the dry environment of the host's cocoon. At this time, spiracles are very prominent on the wasp larva.

The wasp larva immediately begins to spin its own cocoon within the

caterpillar's cocoon and the wasp's cocoon is completed within a few hours. Of the 5,000+ specimens examined for this study, <0.1% had wasp larvae that were outside the host but not yet enclosed in their own pupal cocoons.

The structure of the wasp cocoon indicates that it is spun in a circular (or sideways) manner back and forth from one end of the cocoon to the other, until it is about three layers thick. During this process the wasp larva is visible between the strands of the cocoon. When the cocoon is completed, the wasp larva is no longer visible. The cocoon is dark brown, leathery, oval-shaped, and about 8 mm long. When the cocoon is turned inside out and placed underwater, it takes on the metallic sheen characteristic of an unwettable surface. During the construction of the cocoon, the wasp larva alternately faces anteriorly and posteriorly within the cocoon. But in the final phase of its prepupal stage, the wasp larva always faces anteriorly within the cocoon, i.e., it points its head in the same upstream direction that the caterpillar would have pointed its head.

Because the stage of development cannot be determined until the cocoon is dissected, all specimens within wasp cocoons have been described as pupae. However, within this category, we have identified four phases of development from what we found when the anterior end of the cocoon was opened. First, in the "early" phase, which is actually still part of the larval stage, the larva is still mobile within the cocoon and responds to touch when the cocoon is opened. Morris (1937) referred to this as the eonymphal phase. As development proceeds, the wasp larva begins to transform into the pupal form. The colorless, transparent membranous skin becomes white and opaque. Another change in the larva is the formation of red spots where the compound eyes will form. Differentiation of body regions begins. Morris (1937) referred to this final, immobile, phase as the pronymphal stage.

During the second (or white) phase, three distinct body regions have formed; the head is white and the compound eyes are red. Long legs and long antennae have formed and in females the ovipositor is very well developed. In the later part of this phase, although the head is still white, the thorax becomes black, the eyes dark brown, and wing pads start to form.

The third (or black) phase is characterized by the pupa having a black head, black antennae, black thorax, black legs, a brown and white striped abdomen, and very prominent wing pads. Both the white phase and the black phase are enclosed within a transparent membrane. A meconium is attached posteriorly to the developing pupa (Resh and Jamieson 1988, Fig. 10). These three phases each require about one week. During the fourth (or pre-adult) phase, the wasp pupa has shed the transparent membrane within the cocoon, the meconium has become detached, and the wings are fully expanded.

Adult stage: To emerge from its cocoon, the adult wasp chews a hole dorsally through its cocoon and through the lepidopteran's external pupal case; it does not use the C-slit made by the caterpillar for its own emergence. When the newly emerged wasp comes in contact with the water, an air bubble from

the cocoon surrounds its hairy body. We observed that when an adult female wasp emerged underwater (e.g. in a dish that contained moss and pebbles; we have not observed this in nature), she grasped a sprig of moss with her hind leg and groped in the dish with her other five legs. In another cocoon that was opened underwater, we observed that after a female emerged from the water she gripped the wooden handle of the teasing needle; then, with her hind legs, she wiped down her abdomen and ovipositor and, with her front legs, wiped her head and antennae. A few minutes after drying off, she flew away.

Based on the observations of 575 wasp pupae, the sex ratio of the wasps approaches 1:1 (290 females: 285 males). Some streams, however, had collections favoring females (e.g. Fig. 2, site B, 43:11) or males (e.g. Fig. 2, site F, 8:22; site L, 7:22).

Emergence of wasps begins about two weeks after the unparasitized moths have emerged. Once the moths have emerged from their cocoons, decomposition of their pupal patches begins and lasts for approximately one additional month. The extended duration of the lepidopteran silken patch until the wasps emerge is crucial to the wasps' existence and survival.

Parasitization of the moth larvae varies even on a single rock. For example, 18 lepidopteran patches were collected 23 Jul 1995 from one rock at the mouth of the Clearwater River (Fig. 2, site I). Among these patches: five contained cocoons from which moths had emerged; three held moth larvae, one of which was decomposing and another was parasitized; three were moth pupae, one in an early stage of pupal development and the other two in a later stage with scaled wings; seven specimens were wasp pupae, with three in the early phase, three pre-adults (one male and two females), and one in a damaged condition.

DISTRIBUTION AND PARASITISM

Of 18 sites sampled in the Clearwater River Drainage, *P. confusalis* was found at 13 sites: B, C, D, F, G, H, I, J, K, L, M, N and Q (Fig. 2). *T. pilosa* parasitized *P. confusalis* at eight of those sites: B (55% parasitism 29 Jul 1987, 44% 26 Jun 1988, 5% 3 Jul 1988, 41% 10 Jul 1988, 36% 22 Jul 1993, 45% 14 Jul 1993, 44% 28 Jul 1993, 50% 3 Aug 1993, 35% 11 Aug 1993, 13% 23 Oct 1993, 13% 25 Jul 1994, 29% 5 Jul 1995); C (24% 9 Aug 1987, 5% 26 Jun 1988, 4% 16 Jul 1993); F (58% 22 Jul 1993, 43% 27 Jul 1994); G (41% 28 Jul 1993, 41% 3 Aug 1993, 48% 27 Jul 1994, 47% 23 Jul 1995, 74% 15 Aug 1995, 80% 22 Oct 1995); H (29% 3 Aug 1993, 20% 27 Jul 1994, 50% 5 Jul 1995); I (73% 3 Aug 1993, 64% 27 Jul 1994, 54% 23 Jul 1995); L (35% 22 Jul 1993, 46% 25 Jul 1994); N (75% 22 Jul 1993, 71% 11 Aug 1993, 67% 23 Oct 1993, 48% 12 Jul 1994, 47% 19 Jun 1995, 57% 15 Aug 1995). Variations in rates of parasitism at individual sites may have been caused by sampling of different microhabitats at a site.

What were the characteristics of the sites where either *P. confusalis* or *T. pilosa* were absent? No lepidopterans were found in the cold water (10°C) of the West Fork of the Clearwater River on 28 Jul 1993. Algal patches on the rocks of the warm Marshall Lake outflow (Fig. 2, site O) suggested a lepidopteran population may have been present earlier in the season but had

emerged. The Clearwater River at Highway 83 (R) was sampled on 2 Aug 1993; the water was very cold (11°C) and no moths were found. On 3 Aug 1993 the Blackfoot River at the Russell Gates Fishing Access (J) was sampled. The river was wide, shallow, and swift, and the rocks in the streambed were large, round, smooth and very slippery. The lepidopteran population was very sparse and only 11 specimens could be collected; none were parasitized. The Blackfoot River at the Roundup Fishing Access (K) also had no parasitism in the 49 moths examined. The river here was very deep, wide, and swift. Sampling was limited to a rocky area near the shore.

Samples outside the Clearwater Drainage were also collected during summer 1993. No parasitism was found in a sample taken on 26 Jul 1993 from the outflow of Loon Lake on the Fisher River in Lincoln County, Montana, nor in a sample of 145 specimens taken on 27 Jul 1993 from the Lower Crow Creek above the Lower Crow Reservoir near Pablo in Lake County. Although moth pupae and larvae were abundant in Lower Crow Creek, the water was deep and swift.

Ashley Creek in Flathead County was sampled 30 Jul 1993 at its outflow from Ashley Lake and near the bridge between Lake Monroe and Lone Lake; no parasitism of the moth larvae or pupae present at either site was evident. The patches were extremely calcified and this may have prevented wasps from chewing their way out of their cocoons even if parasitism had occurred. Three sites (S, T, U) in the Swan River drainage system adjacent to the headwaters of the Clearwater River (Fig. 2) sampled on 2 Aug 1993 did not have lepidopteran populations. Algae mats were thick on rocks in the streambed and the water was very slow moving in Holland Lake Creek (T). Although the water was warm at the Lake Lindbergh outlet (U), it was very deep and swift. At site S, the Swan River was deep and wide. There was no parasitism in a sample of 65 specimens collected from Swan River below the dam near Bigfork on 10 Aug 1993. The water there was also deep and very swift.

FACTORS AFFECTING *T. PILOSA* DISTRIBUTION

From the above information, it is apparent that parasitization by *T. pilosa* does not occur in all streams that had *P. confusalis* populations. Reasons underlying this distribution are not readily evident. For example, Lake Inez and Lake Alva (Fig. 2, sites N and Q) are two very similar lakes in the Clearwater River system, with Lake Alva just to the north of Lake Inez in the upper portion of the drainage. Both are warm-water lakes and are surrounded by summer homes. Wooden plank structures dam the outlets of each lake, and the outflow streams have rocky bottoms and banks lined with vegetation. Each stream supports a population of *P. confusalis*. However, parasitization at the Lake Alva outflow is 0% while parasitization at the Lake Inez outflow is 75%.

Why is there such a difference in parasitism when these lake outlets are less than 5 km apart? Water in the Lake Alva outlet flows smoothly (i.e. no

emergent rocks or riffles) over a streambed of uniformly sized rocks that are densely covered with lepidopteran pupal patches. When the water level goes down in late summer, the stream still flows smoothly. However, at Lake Inez, the outflow stream does not have a streambed of uniform composition and the water does not flow smoothly; instead, riffles form from emergent rocks and boulders interspersed among sand and gravel bars. Lepidopteran patches can be found on the large rocks and boulders as well as on small rocks and pebbles. In late summer, the larger rocks project above the water; if the female wasp requires a landing place before she enters the water for oviposition, then the Lake Inez outflow would be a possible habitat whereas Lake Alva would not. Given that the above-described habitats differ in terms of emergent rocks or riffles, and that this was often a feature lacking in sites where moths occurred but parasitism was absent, we suggest that this may be a key feature in determining the local distribution of *T. pilosa*. Perhaps the wasp adult requires emergent rocks to enter the water and remain attached while it searches for a potential host. Our laboratory observations of adults holding on to objects suggest that this is the case.

Owl Creek has characteristics of both Lake Inez and Lake Alva outflows. Riffle regions alternate with pool regions. No parasitism was found in 51 specimens collected 23 Jul 1995 at Owl Creek (Fig. 2, site B) from a pool area located behind a line of rocks across the stream. However, in a riffle area at this site, 22 of the 57 specimens collected were parasitized. The rocks in this riffle area project above water in late summer.

Gustin (personal communication) found a species of *Tanychela* parasitizing populations of *P. confusalis* in the Potlatch River and several of its tributaries in Latah Co, Idaho and in the Palouse River system in Latah County, Idaho, and Whitman County, Washington. The immature ichneumonids found in his study and the unnamed immatures previously reported by Tuskes (1977) in California may also be *T. pilosa*. If the distribution of *T. pilosa* follows that of *P. confusalis*, it would include central California, north to British Columbia and east to Nevada, Idaho, and Montana (Monroe 1972). However, because the type specimen of *T. pilosa* is from Mexico, other species of moths may also be parasitized.

Local factors may also affect distribution. Cool summers may favor the growth and development of the wasp larvae whereas warm summer temperatures may favor the rapid growth of fifth instar caterpillars and, consequently, earlier pupation and emergence. If *T. pilosa* cannot follow the rapid transformation of its host, then it will not be ready for its own pupation.

Because the larval wasp occurs within the caterpillar's body and the moth occurs within an air-filled cocoon (Lloyd 1919), the only aquatic portions of *T. pilosa*'s life cycle are when the wasp adult emerges underwater and then returns to water to lay its eggs. This life history fits even the most narrow definition of an aquatic insect (Hagen 1996). However, like many other para-

sitic insects that occur in aquatic environments, once inside its host the biology of *T. pilosa* more resembles that of a terrestrial insect than an aquatic one.

ACKNOWLEDGMENTS

We thank: Stuart Neff, Temple University, and Brett Merritt, Michigan State University, for assistance in collecting specimens; Jack Stanford and the staff of the Flathead Lake Biological Station of The University of Montana for their assistance and use of facilities; Powder River High School (Broadus, Montana) for use of facilities; the students at Powder River High School for their encouragement to continue this project; Kenneth Hagen and Leo Caltagirone, University of California, Berkeley, for their comments on the manuscript; and Jim Gustin for permission to use his observations. We dedicate our efforts on this study to the late Professor Kenneth Hagen.

LITERATURE CITED

- Bergey, E. A. 1995. Local effects of a sedentary grazer on stream algae. *Freshwat. Biol.* 33:401-409.
- Chapman, R. F. 1982. *The insects - structure and function*. 3rd ed. Harvard University Press, Cambridge.
- Dasch, C. E. 1979. Ichneumon-flies of America North of Mexico: 8. Subfamily Cremastinae. *Mem. Amer. Entomol. Inst.* 29:1-702.
- Elliott, J. M. 1982. The life cycle and spatial distribution of the aquatic parasitoid *Agriotypus armatus* (Hymenoptera: Agriotypidae) and its caddis host *Silo pallipes* (Trichoptera: Goeridae). *J. Anim. Ecol.* 51:923-941.
- Hagen, K. S. 1964. Developmental stages of parasites p. 168-246. In: DeBach, P. (ed.). *Biological control of insect pests and weeds*. Reinhold Publ. Corp., N.Y.
- Hagen, K. S. 1996. Aquatic Hymenoptera. p. 474-483. In: R. W. Merritt and K. W. Cummins (eds.). *An introduction to the aquatic insects of North America*. 3rd ed. Kendall/Hunt Publ. Co., Dubuque, IA.
- Lange, W. H. Aquatic and semiaquatic Lepidoptera. p. 387-398. In: R. W. Merritt and K. W. Cummins (eds.). *An introduction to the aquatic insects of North America*. 3rd ed. Kendall/Hunt Publ. Co., Dubuque, IA.
- Lloyd, J. T. 1914. Lepidopterous larvae from rapid streams. *J. N. Y. Entomol. Soc.* 2:145-152.
- Lloyd, J. T. 1919. An aquatic dipterous parasite, *Ginglymyia acirostris* Towns, and additional notes on its lepidopterous host, *Elophila fulicalis*. *J. N. Y. Entomol. Soc.* 27:263-265.
- McAuliffe, J. R. and N. E. Williams. 1983. Univoltine life cycle of *Paragyraactis confusalis* Walker (Lepidoptera: Pyralidae) in the northern part of its range. *Am. Midl. Nat.* 110:440-443.
- Morris, K. R. S. 1937. The prepupal stage in Ichneumonidae, illustrated by the life history of *Exenterus abruptorius* Thb. *Bull. Entomol. Res.* 28:525-534.
- Munroe, E. G. 1972-1973. Pyraloidea. Pyralidae (in part), p. 1-134, Fasc. 13.1, A-C. In: R. B. Dominick (ed.). *The moths of America north of Mexico*. E. W. Classey Ltd., London.
- Resh, V. H. and W. Jamieson. 1988. Parasitism of the aquatic moth *Petrophila confusalis* (Lepidoptera: Pyralidae) by the aquatic wasp *Tanychela pilosa* (Hymenoptera: Ichneumonidae). *Entomol. News* 99:185-188.
- Tuskes, P. M. 1977. Observations on the biology of *Paragyraactis confusalis*, an aquatic pyralid. *Can. Entomol.* 109:695-699.
- Tuskes, P. M. 1981. Factors influencing the abundance and distribution of the aquatic moths of the genus *Paragyraactis* (Pyralidae). *J. Lepid. Soc.* 35:161-168.
- Ullyett, G. C. 1944. On the function of the caudal appendage in primary larvae of parasitic Hymenoptera. *J. Entomol. Soc. S. Afr.* 7:30-37.